Avian adaptation along an aridity gradient

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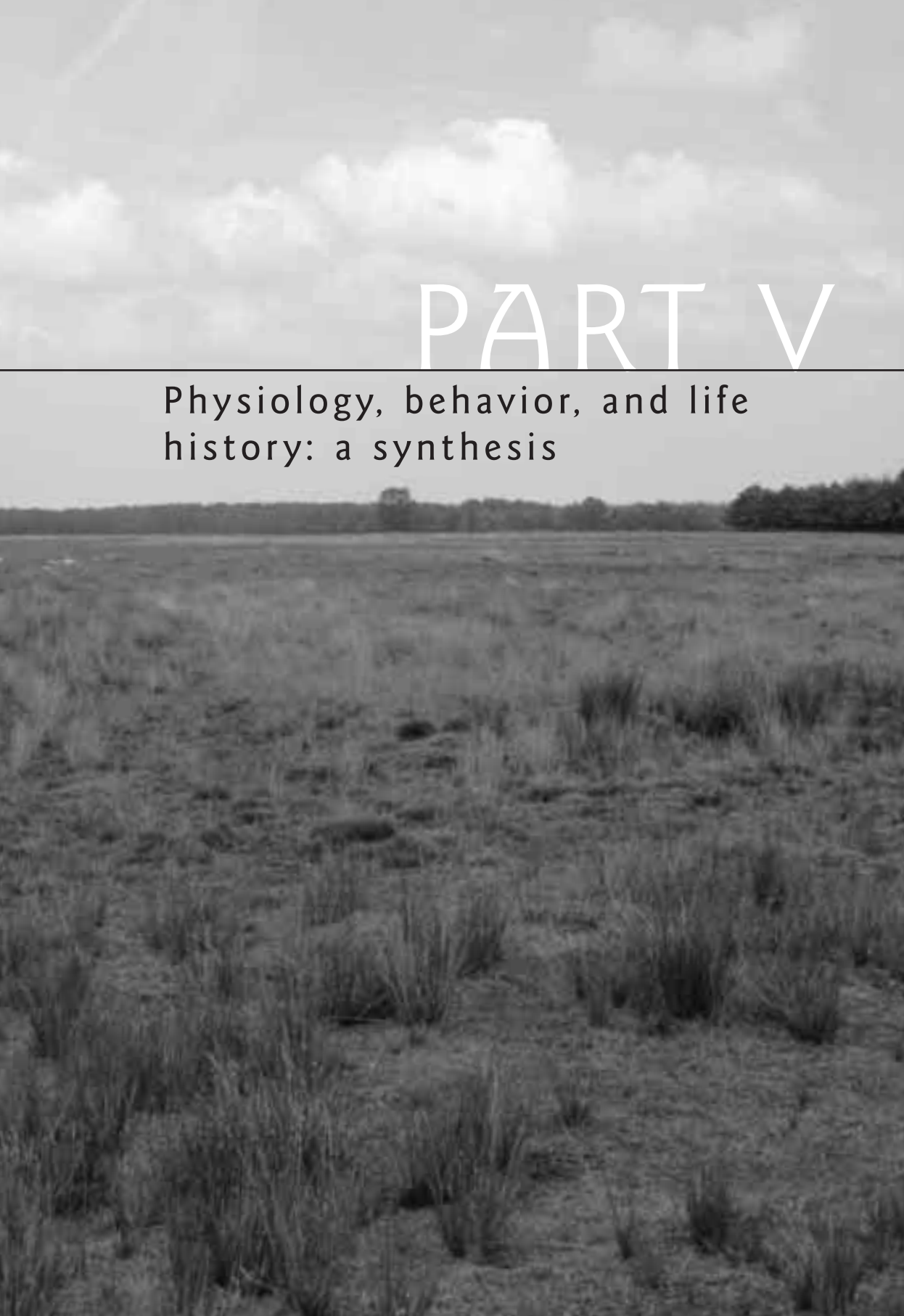

PART V

Physiology, behavior, and life history: a synthesis

CHAPTER 15

Avian adaptation along an aridity gradient: physiology, behavior, and life history

B. Irene Tieleman

Introduction

The theory of natural selection proposes that individuals of a population that are better adapted to the environment than others have a higher evolutionary fitness as measured by the production of descendents, and that as a result their characters dominate within the population or species (Darwin 1859). Acting simultaneously on all properties of an organism, natural selection has resulted in a large diversity of physiological, behavioral and demographic characters among birds. These characters represent components of fitness because they are related to performance in specific environments, and therefore can be viewed as life history variables. The connections between physiology, behavior and demography in the context of environmental variation might provide insights into evolutionary mechanisms that shape life history variation. Still, the relationships between physiological parameters such as metabolic rate and water flux, behavioral strategies like microsite selection and time activity patterns, and demographic variables including growth, reproduction and survival, are poorly understood.

The central prediction of life history theory is that evolutionary fitness is maximized by a trade-off between current and future reproduction (Williams 1966; Stearns 1992). The balance between the fitness costs and benefits of investment in reproduction and in self-maintenance is influenced by the value of the brood and the probability of adult survival. The value of the brood is related to environmental characteristics such as food availability and nest predation, that potentially limit the number of young that can be nourished and determine the probability of raising young successfully. The probability of adult survival is likewise determined by environmental factors, including thermal conditions, food supply and vulnerability to predators, and also by physiological variables such as body condition and aging. Hence, when food supply, predation and other environmental factors vary, the balance between investment in reproduction and self-maintenance is likely to shift. Predictions about the direction of these shifts in different environments can be evaluated by correlations between physiological, behavioral and demographic factors that reflect evolutionary responses.

Attempts to integrate physiology into the demographic theory of life history evolution have focused on the relationship between metabolism and fecundity and mortality. The hypothesis that a higher metabolic rate is associated with higher fecundity but a shorter life span has been supported by some intraspecific studies on birds, but not by others (Calder & King 1974; Ricklefs 1974; Hails & Bryant 1979; Ettinger & King 1980; Bryant & Westerterp 1983; Ricklefs & Williams 1984; Daan et al. 1996). An interspecific analysis including 325 species of birds did not reveal a consistent association between metabolic rate and demographic parameters related to fecundity and longevity, after correcting for body mass and taxonomic affiliation (Trevelyan et al. 1990). Unfortunately, this study used the metabolic rates compiled by Bennett and Harvey (1987) who combined basal

metabolic rates (BMR), strictly defined as minimal energy expenditure of a fasted endotherm in its rest phase at thermoneutral temperatures (King 1974), and metabolism measurements outside this definition, including thermoregulatory costs. Including metabolic rates measured under varying conditions adds substantial variation to the data set and might have confounded analyses. In addition, other physiological variables such as field metabolic rate (FMR) or water flux (WF), integrative measures of energy expenditure and water influx rate of free-living animals measured over a 24-h interval using the doubly labelled water technique (Nagy 1980; Speakman 1997), were not considered by Trevelyan et al. (1990). A more detailed exploration that relates a variety of carefully defined and measured physiological and behavioral variables to variation in growth, reproduction and survival might provide a more powerful test of the putative association between physiological, behavioral and demographic properties.

This paper summarizes the variation in physiology, behavior and demography among a group of closely related species of larks that occur along an environmental continuum of aridity. First, the physiological mechanisms underlying the variation in energy, water and heat balance are explored to identify the selection pressures that are responsible for the physiological variation among larks. Second, I discuss behavioral strategies including microclimate selection and activity patterns in the context of environmental and physiological constraints. Third, I correlate demographic parameters related to growth, reproduction and survival with aridity. And finally, I evaluate our knowledge of the variation in physiology, behavior, and demography in relation to environmental aridity in light of predictions from life history theory. My central prediction is that along a gradient of increasing aridity, decreasing availabilities of energy, water and time limit investments in current reproduction and cause a shift towards investment in self-maintenance. Specifically, I predict that with increasing aridity larks expend less energy and lose less water, grow slower as nestlings, reproduce less frequently, lay smaller clutches, and live longer.

Physiological mechanisms

Physiological variation along an aridity gradient

Lark species that occur along a gradient of increasing aridity have gradually reduced energy and water budgets reflected in lower BMR (Chapter 4, 6) and FMR (Chapter 8), lower total evaporative water loss (TEWL) (Chapter 4, 6) and WF (Chapter 8) (Figure 1a,b). In addition, larks from hot deserts are better able to cope with high ambient temperatures than larks from temperate climates (Chapter 6). The variation in physiological phenotypes of larks along an aridity gradient can not be attributed to acclimation to temperature, food availability or day length (Chapter 5), or to phylogenetic relationships (Chapter 4). The phys-

iological diversity therefore probably results from genetic differences due to natural selection, although future work is required to investigate the role of developmental plasticity.

Mechanisms to reduce metabolism

Several authors have proposed that interspecific variation in FMR and BMR may be attributable to variation in organ size, because tissue-specific metabolic rates of organs such as heart, brain, liver and kidney are relatively high (Kersten & Piersma 1987; Daan et al. 1990; Chappell et al. 1999). Large organs presumably provide the machinery for a high metabolic output in the field, and result in high BMR. This thesis does not support this hypothesis at the interspecific level: desert lark species do not have smaller organs than mesic larks depite their reduction in BMR of about 50% and in FMR of 24-39% (Chapter 5, 8). However, at the intraspecific level variation in BMR resulting from acclimation to different environmental conditions is at least partly correlated with the size of intestine, liver, kidneys and stomach (Chapter 5, 8). Alternative mechanisms that might underlie the reduction in BMR with increasing aridity are lower tissue-specific metabolic rates and lower energetic costs of the immune system. Low tissue-specific metabolic rates have the advantage of minimizing energy requirements and heat production, while large organs can be maintained to act as water reserves for periods of acute heat stress. A gram of protein tissue not only contains more water than a gram of fat, protein metabolism also produces less heat per unit water than fat metabolism. If the immune system requires significant input of energy, birds living in desert environments, where the risk of infection may be low, may have relatively low metabolic costs to maintain adequate immunity. Unfortunately, our understanding of the energetic costs of maintaining an immune system is still rudimentary (Lochmiller & Deerenberg 2000).

Mechanisms to minimize water loss

The literature contains a number of suggestions for mechanisms that might reduce TEWL in desert birds. Counter-current heat exchange in the nasal passages of some species can ostensibly recover significant quantities of water from the exhaled air stream, thus lowering respiratory water loss (Schmidt-Nielsen et al. 1970). A number of authors have suggested that hyperthermia, the elevation of body temperature 2-4 °C above normal, can reduce TEWL (Calder & King 1974; Weathers 1981; Dawson 1984; Withers & Williams 1990). A third mechanism suggested to reduce TEWL is the adjustment of the lipid structure and composition in the skin affecting cutaneous water loss (Menon et al. 1989; Menon et al. 1996).

In larks from deserts reductions in water loss rates at moderate air temperatures are not the result of more efficient counter-current heat exchange in the nasal passages (Chapter 10), or of hyperthermia (Chapter 6, 11), but appear attributa-

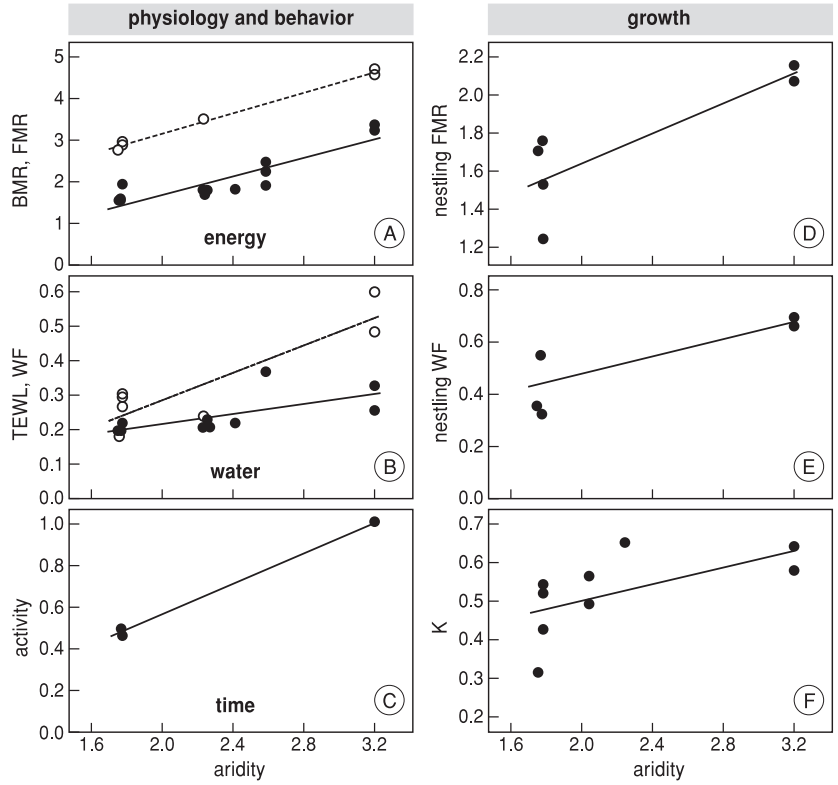

Figure 1. Physiology, behavior, growth, reproduction, and survival of larks along an aridity gradient. Solid and hatched lines represent regression equations through the data. Grey lines stand for hypothesized relationships. Original data can be found in the appropriate chapters or in the text. a. Basal metabolic rate (BMR, kJ d^{-1} $g^{-0.884}$, filled symbols, solid line, Chapter 4) and field metabolic rate (FMR, kJ d^{-1} $g^{-0.879}$, unfilled symbols, hatched line, Chapter 8). b. Total evaporative water loss (TEWL, g d^{-1} $g^{-0.770}$, filled symbols, solid line, Chapter 4) and field water flux (WF, x 3, g d^{-1} $g^{-0.730}$, unfilled symbols, hatched line, Chapter 8). c. Proportion of total day-time spent active. d. Field metabolic rate per nestling (kJ d^{-1} g^{-1}, Chapter 8). e. Field water flux per nestling (g d^{-1} g^{-1}, Chapter 8). f. Growth constant K ($days^{-1}$, Chapter 8).

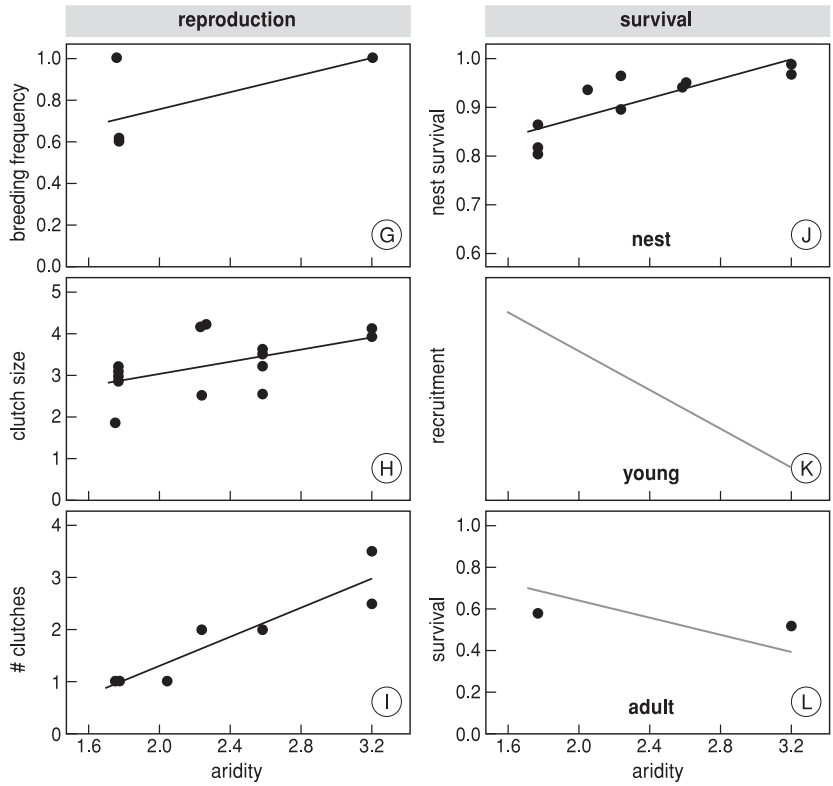

Figure 1 (continued). g. Average number of breeding seasons per year. h. Average clutch size (Chapter 8). i. Average number of clutches per breeding season (Chapter 8). j. Probability of daily nest survival (day^{-1}, Chapter 8). k. Survival of young from fledging to recruitment in the breeding population as predicted from the length of the post-fledging parental care period. l. Probability of adult survival (year^{-1}) for Hoopoe Larks and Skylarks. Dotted line represents hypothesized relationship between survival and aridity.

ble to differences in cutaneous water loss, possibly influenced by the lipid composition of the epidermis and changes in the vascularization of the skin (Chapter 7). Cutaneous water loss constitutes 50-70% of TEWL in larks at moderate air temperatures (Chapter 7). The suggestion that low metabolic rates are correlated with low ventilation rates and therefore should result in reduced respiratory water loss (Dawson 1982), is not supported by our findings that larks from arid environments have similar mass-specific values of respiratory water loss despite lower metabolic rates compared with species from mesic areas (Chapter 7).
Skin lipid structure and composition and skin vasodilation can probably vary independently of metabolism, ambient temperature, and body temperature, and thereby provide flexible mechanisms to adjust cutaneous water loss depending on environmental conditions or physiological state. In contrast, counter-current heat exchange and hyperthermia are less efficient and appear to have disadvantageous side-effects. Empirical evidence shows that counter-current heat exchange in the nasal turbinates saves only 10% of TEWL in Crested Larks and 0% in Desert Larks measured at 25 °C instead of the predicted 49%, and that its effectiveness decreases when ambient temperature increases (Chapter 10). Hyperthermia would presumably only be used during short time periods and might affect not only water loss but also protein structure and enzyme function. A higher body temperature setpoint would require a permanently increased metabolism.

Mechanisms to cope with heat

The combination of a low metabolic heat production and a low dry heat transfer coefficient enables larks from deserts to better cope with high ambient temperatures than species from mesic areas (Chapter 6). The dry heat transfer coefficient is a complex variable that combines the effects of feather insulation, skin vasodilation and surface to volume ratios. The common body shape of all larks suggests that the latter factor can not explain the interspecific variation. It will be interesting to investigate the first two components in the future.

Evolutionary significance

The mechanisms that underlie the variation in physiological phenotypes among larks suggest that in arid environments three selection pressures act independently and simultaneously: lack of water, food scarcity, and high ambient temperatures. Larks from deserts have evolved a mechanism to reduce water loss that functions independently of metabolism and body temperature. This suggests that the frugal water economy of desert species is not merely a byproduct of constraints on the energy balance, but an adaptation to water scarcity per se. In addition, the reduction in metabolism potentially is accomplished without compromising the water storage capacity of the internal organs. Low food availability is presumably the selective agent responsible for the reduced energy requirements

and concurrent low expenditure in arid environments. Low metabolic heat production is also favorable in light of the high ambient temperatures that have apparently selected for a reduced dry heat transfer coefficient.

Behavioral strategies

Variation in behavior along an aridity gradient

The time available per day for activities such as foraging or providing for young depends on the time of the year, the thermal conditions and the food availability. During spring, we observed that larks in temperate areas can be active during the entire daylight period, whereas species in hot deserts, such as Hoopoe Larks (Chapter 14) and Bar-tailed Desert Larks (unpublished data), are forced to spend the middle part of the day inactive in the shade to avoid overheating (Figure 1c). Consequently, temperate-zone larks can invest more time per day in raising offspring than species in deserts.

Behavioral mechanisms and adaptive significance

Larks in the desert spend the middle part of the day inactive in sites with favorable microclimates to avoid overheating (Chapter 13, Chapter 14). This behavioral pattern indicates that the thermal environment presents a constraint on the time available for activity. In addition, the selection of relatively cool microsites probably reduces water requirements for evaporative cooling (Chapter 13). A period of inactivity during the day also reduces energy expenditure and thereby food requirements. In response to an experimental increase in food availability Hoopoe Larks reduced the time spent foraging, increased the time spent inactive during the middle part of the day, and increased the time devoted to maintenance activities such as preening (Chapter 14). With access to extra food, they started and ended their midday shading period when temperatures were lower than when they had no access to supplemental food. These results indicate that the desert environment poses constraints on food and water intake, foraging time, and thermoregulation. In addition, they show that birds optimized the time spent foraging and thermoregulating depending on a combination of physiological state variables including body temperature, hydration state and level of energy reserves.

Demography along an aridity gradient

Growth

Nestling growth rate bears a relation to evolutionary fitness through energy and nutrient requirements of growing young and through survival of offspring to the end of the growth period (Lack 1968; Ricklefs 1979) and is thus an important component of the life history of species. The growth rate constant K ($days^{-1}$) of

the logistic equation provides an overall measure of weight increase and is commonly used to express growth rate (Ricklefs 1979). In a data set including nine species of larks, growth rate decreased along a gradient of increasing aridity (Chapter 8, Figure 1f). What determines growth rate in birds is not completely understood, and suggestions vary from physiological and structural constraints (Ricklefs 1979; Starck & Ricklefs 1998) to ecological factors such as food supply and nest predation (Lack 1968; Perrins 1977; Lima 1987). Physiological and structural constraints may vary between species with different developmental strategies such as altricial and precocial birds, but are unlikely to explain the variation within a group of closely related species with similar development patterns such as the lark family. Along a gradient of increasing aridity, and concurrent decreasing resource availability, food and water supply forms a more likely explanation for the decrease in growth rate. However, an effect of nest predation can not be excluded and future research will be required to identify the mechanisms responsible for the variation in growth rates among larks from diverse environments.

Environments where food and water are in short supply might favor young with low energy and water requirements not only for growth, but also for metabolism, evaporation and excretion. In support of this hypothesis, mass-specific FMR of 6-8 day old nestlings of six species of larks decreases with increasing aridity (Chapter 8, Figure 1d). A similar pattern of decreasing mass-specific water flux with increasing aridity was marginally insignificant ($P = 0.057$) (Chapter 8, Figure 1e). Based on these regression analyses, nestlings in hyperarid deserts are estimated to expend on average 28% less energy for metabolism and lose on average 37% less water than counterparts in mesic habitats.

Reproduction

Understanding life history variation among species along an aridity gradient requires knowledge of timing and intensity of reproductive periods during an individual's life time. This section describes the frequency of reproduction as the number of breeding seasons per year, and the intensity of reproduction per breeding season measured by clutch size and number of clutches.

In temperate zones, birds breed each spring, yet in many arid-zone environments breeding depends on rainfall that is generally low and can be unpredictable (Immelmann 1973). Information on the frequency of reproduction of individual larks from varying environments is limited, evoking the need to use population-level measures, such as the proportion of birds with territories that breed in a given season.

From 1998 to 2002 we monitored the breeding activities of Hoopoe Larks in the Arabian Desert, and found that reproduction is related to rainfall (Figure 2). Hoopoe Larks are present in the nature reserve Mahazat as-Sayd year-round, but

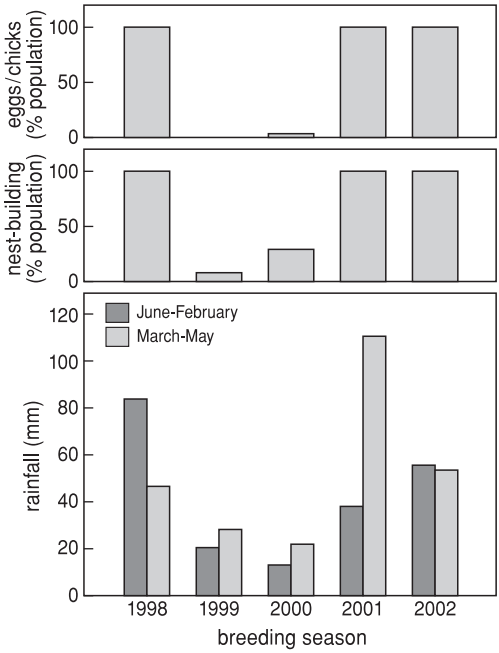

Figure 2. Nest-building and tending nests with eggs or young by Hoopoe Larks in relation to rainfall in Mahazat as-Sayd, Saudi Arabia, during the period 1998-2002. Total rainfall per breeding season is separated in rain prior to the breeding season (June-February) and during the breeding season (March-May).

their breeding activities are seasonal and restricted to the period February-June. Observations of colorbanded birds show that at least some individuals stay in the same territory for a minimum of four consecutive years. Our core study area consists of about 35 territories that were occupied by territorial Hoopoe Lark pairs each spring. Territories are large, about 0.4-0.5 km^2, and the spatial pattern of rainfall frequently causes variation among territories even within the study area. In two years following low winter rainfall, 1999 and 2000, the majority of the population did not attempt to breed (Figure 2). In 1999, two females responded to a late and local spring rain by building nests, but they did not initiate egg-laying. In 2000, ten females were observed nest-building after a small rain, but most individuals did not complete their nests and only one of these birds layed eggs. Food availability and temperature interact to form a window of breeding opportunity for the birds in the Arabian Desert. Early in the season the threshold of food supply required to meet the requirements of growing young and of self-maintenance is relatively low. In the course of the season the threshold level of

food supply increases because time available for foraging decreases as a result of higher temperatures (Chapter 14). During drought years the minimum threshold of food supply is not reached, and birds do not breed at all.

I collated observations on breeding frequency of different species of larks and found a decrease with increasing aridity (Figure 1g). The patterns of breeding activities in relation to rainfall of Bar-tailed Desert Larks and Dunn's Larks, two other species that are present year-round in Mahazat as-Sayd, are identical to that of Hoopoe Larks during the period 1998-2002 (personal observation). In contrast, during the period 1989-1993 Dune Larks in the Namib Desert bred each year at predictable times, between December and March, despite complete lack of rainfall during these years (Williams 2001). Yearly breeding activities are also found in Woodlarks and Skylarks in the temperate zones. Unfortunately information on breeding frequencies of semi-arid larks is difficult to interpret due to its qualitative nature (Maclean 1970a; Lloyd 1999). Breeding densities of resident insectivorous larks in the semi-arid Nama Karoo in South Africa vary with rainfall; fewer nests are found in dry years (Lloyd 1999). The granivorous nomadic lark species in South Africa disappear from areas in drought years and appear in areas that have received rain, where they can breed at any time during the year (Maclean 1970a; Lloyd 1999). The lack of information on movements of individual birds or even populations of these nomads precludes an estimate of their breeding frequency.

The intensity of reproduction in years that larks breed can be measured by the clutch size and the number of clutches per breeding season. Clutch size varies among and within species but decreases when the environment becomes more arid (Chapter 8, Figure 1h). Based on a regression of clutch size as a function of aridity (Figure 1h), I calculated that larks in hyperarid deserts have an average clutch size of 2.8 eggs, whereas species in mesic areas lay an average of 3.9 eggs. In addition, the number of clutches per breeding season decreases with increasing aridity from an average of three per year in mesic habitats to one per year in hyperarid deserts (Chapter 8, Figure 1i). Hence, the total number of eggs produced per breeding season averages 2.8 for larks in hyperarid deserts and 11.7 for species in mesic environments, more than a four-fold difference in intensity of reproduction.

A trade-off between current and future reproduction assumes that the annual reproductive investment is associated with fitness costs (Williams 1966; Stearns 1992). Although these costs are difficult to quantify, they might be approached by indirect measures. If the reproductive investment is correlated with parental effort as measured by energy expenditure, water loss and clutch size, then the reproductive value of a single brood should be lower for an arid-zone species than for a lark from mesic habitats (Chapter 8). This hypothesis leads to the prediction that fewer young are recruited into the breeding population per year in arid

habitats than in mesic environments, and that an adult arid-zone lark should have a higher annual survival than an adult of a mesic-zone species.

Survival

The investment in current reproduction should depend on the probabilities that the reproductive attempt will successfully produce offspring and that the parents will have other opportunities to reproduce in the future. Defining successful production of offspring as recruitment into the breeding population, and assuming that all larks can reproduce in the first breeding season after hatching, recruitment depends on nestling mortality and post-fledging survival. The chance of future reproduction for parents is largely determined by the probability of survival to the next year, although body condition may also play a role.

Nest predation increases with increasing aridity and causes a higher nestling mortality in deserts (Chapter 8, Figure 1j). The probability that a lark nest survives until fledging in a hyperarid environment is about 2%. In contrast, 87% of the nests in mesic habitats successfully produce fledglings. The probability of nestling survival does not only depend on nest predation but also on food provisioning by the parents. Woodlarks and Skylarks in mesic areas normally provide sufficient food to successfully rear all nestlings in a brood. In contrast, at least one chick starved to death in the majority of nests of four species of larks in the Arabian Desert (Chapter 8). Although insufficient information precludes the incorporation of renesting attempts in the pattern, it is obvious that the combination of clutch size, number of clutches, nest survival, and nestling starvation results in a yearly production of fledglings that markedly decreases with increasing aridity.

Quantitative information about the probability of fledgling survival is not available, but an indirect estimate of recruitment can be made using the post-fledging parental care period of various species. Post-fledging parental care has been measured in few lark species, but data on Skylark (6 days (Cramp 1988)), Short-toed Lark (1-3 weeks (Cramp 1988)), Dune Lark (3 weeks, J.B. Williams personal communication), and Hoopoe Lark (> 1 month, Cramp (1988) and personal observation) suggest that the parental care period is longer when environments are more arid (Figure 1k). If post-fledging parental care is an index of fledging survival, recruitment is higher in arid environments.

Considering that arid-zone larks do not breed each year and invest less in reproductive attempts during a breeding season (Chapter 8), one might expect that adult survival is higher in these species than in larks from temperate zones (Figure 1l). The probability of annual survival of adult birds can be measured by monitoring individually marked birds over the course of several years, information that is available for few lark species. The literature contains several estimates of annual survival for Skylarks in Europe (Delius 1965; Spaepen 1991;

Schläpfer 1988; Wolfenden & Peach 2001), but the study of Wolfenden and Peach (2001) seems by far the most robust. These authors have monitored a population of colorbanded Skylarks in a dune area near Liverpool for twenty years and used mark-recapture models to estimate survival, taking into account the probability of recapture. Annual survival rates of Skylarks increased from around 0.39 during 1980-1985 to 0.66 during 1995-1998, with an average of 0.51 (SE 0.024) over the entire study period (Figure 11). An estimate for the Hoopoe Lark, a species at the arid extreme of the aridity gradient, comes from four years of colorbanding birds in our study population in the Arabian Desert (Figure 11). To my knowledge this is the first estimate of annual survival for a desert bird. Using resightings of marked individuals in a mark-recapture model, we calculated that the probability of survival was 0.58 (95% CI: 0.33 - 0.80) with a higher value for males (0.65) than females (0.34) (Tieleman, Williams and Doherty, unpublished data). Because these models assume that missing birds are dead while they might have permanently emigrated from the study area, the differences in survival estimates between sexes might indicate that females move over larger distances than males. Survival estimates for other larks are not available, but anecdotal information on longevity of 3 individuals shows that Dune Larks in the Namib Desert can live for at least 6 years (Williams 1992). Evaluation of the hypothesis that adult survival increases with increasing aridity awaits future work on larks from arid, semi-arid and mesic environments.

Life history evolution along an aridity gradient

Predictions from life history theory are based on the central tenet that evolutionary fitness is maximized by a trade-off between current and future reproduction (Williams 1966; Stearns 1992). The balance between current reproductive investment and self-maintenance is reflected in their inverse relationship and is responsive to environmental conditions that affect expectations of reproductive success and adult survival. Along a gradient of increasing aridity, with concurrent decreasing availabilities of energy, water and time, I hypothesized that the environment limits investments in current reproduction causing a shift in favor of investment in self-maintenance.

The physiological and behavioral adaptations of larks along an aridity gradient indicate that food supply, water availability and thermal environment constitute selection pressures that presumably also act on growth, reproduction and survival. With increasing aridity less energy, water and time are used by the parents during the reproductive season, nestling energy and water requirements are reduced and growth is slower, reproductive effort measured by clutch size and number of clutches decreases, yearly reproductive success is lower, and adult annual survival is presumably higher. These correlations between physiology, behavior,

demography and environment are consistent with predictions from life history theory, and open up the challenge to understand the mechanisms that link physiology and behavior directly to growth, reproduction and survival.

The physiology of growth has been extensively studied, but although we have gained insights into the differences between development strategies of the extremes of the precocial-altricial spectrum (Starck & Ricklefs 1998), the cause of variation in growth rate among closely related species with similar development remains an enigma. An important step will be to determine whether the variation in growth rates among larks results from genetic differences or from phenotypic plasticity. One might expect a role for food in explaining the variation in growth rates along an aridity gradient, perhaps through levels of essential nutrients (Ricklefs 1979).

Physiological variables such as body condition and hormone balance probably play an important role in the timing and intensity of reproduction. How predictable environmental factors such as daylength and seasonal changes in temperature interact with unpredictable factors such as rain and food supply to form a window of breeding opportunity in arid environments is poorly understood (Hau 2001). An integrative approach that combines energetics and endocrinology with behavior under varying environmental conditions may be required to explore the cues that trigger the onset of breeding and determine the motivation of parents to tend their eggs and young.

A plethora of behavioral and physiological factors has been proposed to affect adult survival, some based on experimental studies, others based on correlative evidence. Mortality as a result of predation may be related to activity patterns, or to nest microsite selection that influences the exposure of incubating parents (Ricklefs 1969; Martin 1993). Low BMR and FMR may cause a lower risk of starvation or poor body condition through reduced food requirements. Reduced metabolism also could result in a slower build up of oxygen free radicals that cause deterioration of physiological processes and thereby influence aging. In these cases low BMR and FMR correlate with each other and with high investments in self-maintenance. In contrast, studies focusing on individuals within a species have attributed low BMR to low levels of self-maintenance and high investments in reproduction (Deerenberg et al. 1998; Wikelski et al. 1999). Low levels of metabolism in arid environments may also be explained by an energetically inexpensive immune system in environments where vectors for parasites are scarce. A better understanding of survival along an aridity gradient will benefit from future work on the relationship between predation risk and behavior, and on the interaction between metabolism, immune system and body condition.

The challenge for the future will be to further integrate physiology and behavior into the demographic theory of life history evolution in order to increase our understanding of causation and function of life history variation. The major

obstacle will be to overcome the different time scales of evolved and individual responses. Therefore, a combination of comparative studies, modeling, and experiments might prove most fruitful to explore patterns of phenotype-by-environment correlation, to illuminate mechanisms underlying these patterns, and to connect trait values with fitness.